Melanism in *Phigalia titea* (Cramer) (Lepidoptera: Geometridae)

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Abstract: Data are presented on the occurrence of the typical and melanic forms of *P. titea* (Cramer) in Leverett, Massachusetts from 1968–1970. Leverett is located in a rural area, where lichens abound on trees which are not noticeably darkened by soot. Melanics comprised 20.4% of the sampled *P. titea* population (491 individuals). Melanic percentages varied little from year to year, and from week to week within each year. However, melanic moths were taken most frequently during the first hour of activity in the evening. In 1969 and 1970, *P. titea* of both forms were color-marked as they rested at lights. Total recapture percentages of the typical and melanic forms were not significantly different. The implications of these results are discussed with reference to the widely-accepted explanation of industrial melanism in England.

The spread of melanism among many moths of Europe and North America is providing an unprecedented opportunity for studying evolution in action. Since the mid-1800's in England and Europe, and more recently in North America, many geometrid and noctuid species have exhibited a dramatic increase in the occurrence of melanic forms. From the extensive studies of Kettlewell and his associates, particularly on *Biston betularia* (L.) (Geometridae) in England, the folowing major findings have emerged: 1. melanism is usually controlled by a single gene, the allele for black ordinarily being dominant to that for pale or typical coloration (Kettlewell, 1959); 2. melanic individuals appear to be more viable than typicals (Ford, 1937, 1964; Kettlewell, 1958a), and may exhibit other behavioral and physiological differences—e.g. in larval habits (Kettlewell, 1958a, 1961), courtship and mating (Kettlewell, 1957), and background selections (Kettlewell, 1955a); 3. melanic forms have increased in relative abundance in recent times, particularly in industrial areas (Kettlewell, 1958b); 4. melanic individuals are at a selective advantage in industrial areas, and at a selective disadvantage in rural areas, when compared with typical individuals; and differential predation by birds on the two forms contributes significantly to the selective advantage or disadvantage observed (Kettlewell, 1955b, 1956).

A general explanation for industrial melanism, emphasizing the cryptic advantage of melanics in industrial areas (Kettlewell, 1958a), has now gained wide acceptance. In this view, melanics are favored wherever air pollutants act to darken tree trunks through the killing of epiphytic lichens and the deposition of soot. Ample experimental data support this explanation in the case of *B. betularia* (for an extended review of this topic, see Ford, 1964).

There are, however, a number of findings which suggest that an explanation based on cryptic advantage may not suffice for all instances of increased melanism. Thus, for example, while most cases of recent melanism involve bark-like cryptic insects, at least one warningly-colored beetle, *Adalia bipunctata* L., is displaying an increase in melanic frequencies in industrial areas (Creed, 1966). Another problem is posed by the extent of melanism in ostensibly rural areas (i.e. where the trees are not devoid of lichens, and are not noticeably darkened by soot). The present study area in Massachusetts is an example. Here melanic frequencies are high in several geometrids, and these melanics, like their typical counterparts, prefer light backgrounds (Sargent, 1968, 1969)—a preference which would seem to put them at a considerable cryptic disadvantage. A further difficulty is posed by the recent finding that a steep cline exists in the melanic frequencies of *Gonodontis bidentata* Clerck (Geometridae) across the city of Liverpool (Bishop and Harper, 1970).

These last few studies suggest that the incidence of melanism in some cases may be related to effects of industrialization other than observable environmental darkening. Possible pollution effects on the insects, perhaps acting on the larvae through chemical contamination of the vegetation, would seem to warrant further investigation in this regard. It may be that the superior viability of melanics, stressed some years ago by Ford (1937, 1940), has been generally underestimated in recent discussions regarding the selective advantage of melanism. Older ideas attributing melanic success in industrial areas to relaxed selection pressure from predators might also bear some re-examination in light of these recent findings.

The relatively recent rise and spread of melanism among North American moths (Owen, 1961, 1962) may provide opportunities for study which are no longer available in England and Europe. Thus far, however, few studies have been carried out. Klots (1964, 1966, 1968a,b) has described increasing melanism among noctuids in Connecticut, and has conducted some breeding studies on the species involved. Kettlewell (1965) has provided a genetic analysis of crosses involving *Biston betularia* and the North American *B. cognataria* (Guenée). Sargent (1966, 1968, 1969), on the basis of experimental studies of background selections, has suggested that some North American melanics may not yet have evolved appropriate background preferences, as *B. betularia* in England appears to have done (Kettlewell, 1955a).

There is need for carefully acquired data on melanism in North America, and the present study is an attempt to gather such data over a period of years in an area where increasing industrialization, and consequent increasing environmental pollution, seem likely. It is hoped that this study will serve to stimulate others to obtain similar data in their areas; provide accurate data for later comparative purposes; and increase our knowledge and understanding of the entire phenomenon of industrial melanism.

METHODS

The present report summarizes data obtained on wild-caught Half-wing Geometers, *Phigalia titea* (Cramer), in Leverett, Massachusetts during the springs of 1968, 1969, and 1970. Leverett is located some 75 air-miles west of Boston, 25 air-miles north of Springfield, and 37 air-miles east of Pittsfield. The study area shows little visible evidence of industrialization—lichens abound on trees which are not noticeably darkened by soot. Leverett apparently receives little air-borne pollution from the west (the direction of the prevailing wind), as Albany, New York (66 air-miles away) is the closest large industrial center in that direction.

The melanic form of *P. titea*, f. *deplorans*, was described by Franclemont (1938), and its historical occurrence in North America has been discussed by Owen (1962). All *P. titea* obtained were easily assigned to either the typical or melanic morph, as no intergrades between the two were noted in the study area. (Figures of both morphs may be found in Remington (1958)).

The moths were collected at four 150 watt Westinghouse outdoor spotlights. In 1969 and 1970, an additional 15 watt black light fluorescent tube at my home was used. Only males were obtained, as females of *P. titea* have rudimentary wings and are not taken at lights. Most of the moths were either used in background selection experiments and subsequently sacrificed (1968), or marked as part of a mark/recapture study (1969, 1970). In the latter case, the lights were usually checked at half-hour intervals, and newly arrived moths were color-marked at each check.

In the mark/recapture study, moths alighting near the lights were marked as they rested with a small spot of Flo-Paque paint, applied with a fine brush, on one of their forewings. Marking was carried out on all but nights of heavy rain, when many moths were washed into puddles under the lights. A different color was used each night during the study in both years. The marked moths were then sought at the lights on subsequent nights, and were collected upon their return. Some of these recaptured moths were then marked and released again in order to see whether they might return, but no moths were recaptured a second time.

These procedures differ in two ways from those used in prior mark/recapture experiments (e.g. Kettlewell, 1955b, 1956; Kettlewell and Berry, 1969). First, individuals were marked on the upper surface of the wings, rather than the underside, eliminating any need to anesthetize or handle the moths, but also perhaps introducing some effects on visual predation. Second, no laboratory-reared individuals were released into the study area, eliminating any unusual

Table 1. Total numbers of typical and melanic *P. titea* taken over three years in Leverett, Mass.

	Years			
Forms	1968	1969	1970	Totals
Typical	125	135	131	391
Melanic	44	26	30	100
% Melanic	26.0	16.1	18.6	20.4

predation effects which might result from artificially dense populations of prey, but also placing definite limits on sample size.

The data obtained in these studies were amenable to analysis by chi-square 2 × 2 tests, and all values of chi-square presented with the results were obtained in this manner.

ANALYSIS OF CAPTURES

A summary of the occurrence of typical and melanic *P. titea* over three years is presented in Table 1. The ratio of typical/melanic individuals varied little from year to year, with melanics averaging 20.4% of the population. Melanic numbers, relative to typicals, were higher in 1968 than in 1969 (chi-square 4.82, P less than 0.05), but no other differences between years were found (1968/1970, chi-square 2.60, P greater than 0.10; 1969/1970, chi-square 0.35, P greater than 0.50). Thus, no trend of increasing or decreasing melanism was discernible over this period.

Table 2. Numbers of typical and melanic *P. titea* taken by weeks over three years in Leverett, Mass.

	Typical/Melanic (% Melanic)			
Weeks	1968	1969	1970	Totals
March 25–31	66/8 (10.8)	—	—	66/8 (10.8)
April 1–7	37/25 (40.3)	48/9 (15.8)	—	85/34 (28.6)
April 8–14	14/2 (12.5)	74/14 (15.9)	74/17 (18.7)	162/33 (16.9)
April 15–21	8/7 (46.7)	13/3 (18.7)	23/4 (14.8)	44/14 (24.1)
April 22–28	0/2 (100.0)	—	31/8 (20.5)	31/10 (24.4)
April 29–May 5	—	—	3/1 (25.0)	3/1 (25.0)

TABLE 3. Numbers of typical and melanic *P. titea* taken by hours over two years in Leverett, Mass.

Hours[1]	Typical/Melanic (% Melanic) 1969	1970	Totals
7:00–8:00 PM	13/6 (31.6)	39/13 (25.0)	52/19 (26.8)
8:00–9:00 PM	48/10 (17.2)	40/5 (11.1)	88/15 (14.6)
9:00–10:00 PM	32/5 (13.5)	25/4 (13.8)	57/9 (13.6)
10:00–11:00 PM	21/4 (16.0)	10/2 (16.7)	31/6 (16.2)
11:00–12:00 PM	7/0 (0.0)	0/1 (100.0)	7/1 (12.5)

[1] Eastern Standard Time.

The numbers of typical and melanic individuals taken each week of the season for three years are given in Table 2. Although the weekly typical/melanic ratios were variable, there were no trends indicating a relative increase or decrease of either form with the advance of the season.

Table 3 presents the ratios of typical/melanic individuals taken each hour of the evening over two years. In both years, relatively more melanics were taken during the first hour of activity than during all later hours, and this difference was significant for the combined data of the two years (chi-square 5.55, P less than 0.02).

MARK/RECAPTURE EXPERIMENT

The numbers of *P. titea* marked and recaptured during two years are presented in Table 4. Over both years, the numbers of typical and melanic moths recaptured, relative to the numbers of each that were marked, were not significantly different (chi-square 0.42, P greater than 0.50).

Most of the recaptures were made on the first night following the night of

TABLE 4. Results of mark/recapture experiments with *P. titea* over two years in Leverett, Mass.

Forms	Number Marked 1969	1970	Total	Number Recaptured 1969	1970	Total	Percent Recaptured 1969	1970	Total
Typical	131	107	238	11	7	18	8.4	6.5	7.6
Melanic	23	24	47	4	1	5	17.4	4.2	10.6

marking (11 typicals, 61%; 3 melanics, 60%). Other recaptures occurred on the second (1 typical, 1 melanic), third (5 typicals), and fifth (1 typical, 1 melanic) nights following marking.

DISCUSSION

The extent of melanism in *P. titea* recorded here (20.4%) is more than double any reported by Owen (1962) for this species. This difference may reflect a real difference between the present study area and those Owen sampled, or may be due to a general increase in melanism since the time of Owen's surveys. Unfortunately, data permitting distinction between these alternatives are not available. Such a situation emphasizes the desirability of obtaining data on melanism for many years in a given locality.

If melanic *P. titea* were at a cryptic disadvantage to typicals in the present rural study area, one might expect melanic percentages to decrease with seasonal advance (assuming no differences between typicals and melanics in terms of emergence time or longevity). However, data over three years gave no evidence of such a decrease, suggesting that whatever predation occurs is not highly selective between the typical and melanic moths. These same data tend to dispel the idea that melanics eclose early, before the return of many insectivorous birds, in species which are on the wing in the early spring. If this were true, one would expect to record higher percentages of melanics earlier in the season, and the data show no such trend.

Results of this study do indicate that melanic *P. titea* are more commonly taken at lights very early in the evening than at any later time. While the significance of this early activity on the part of melanics is obscure at present, the phenomenon warrants further investigation. Certainly it now seems advisable to record the time of night whenever sampling for melanics is carried out.

The present mark/recapture experiment revealed no significant difference between the recapture percentages of typical and melanic moths. This result differs from that obtained by Kettlewell (1956) in a mark/release/recapture experiment involving typical and melanic *Biston betularia* in a rural area in England, where typicals were recaptured at twice the level of melanics.

Experiments of this sort are rather crude, and with small sample sizes, one expects negative results unless one morph is at a considerable selective advantage over the other. Typicals were apparently at such an advantage in the *B. betularia* situation studied by Kettlewell, but no evidence for any such advantage was obtained with *P. titea*. A larger sample of marked *P. titea* should be obtained, but at present it appears that any selective advantage of either adult morph must be rather small. This may indicate that differential selection operates most strongly on some earlier life cycle stage, and that the present sample of marked adults was already a product of such differential selection.

It is interesting to note that despite some differences in procedure, the recapture patterns and percentages obtained in the *B. betularia* and *P. titea* studies were comparable. No anomalous recapture patterns, like the first-night deficit described by Kettlewell et al (1969) in some populations of *Amathes glareosa* (Esper) (Noctuidae), were noted.

The over-all results of the present study suggest that the factors responsible for melanism in *P. titea* may be different than those described for *B. betularia* in England. The substantial melanism recorded here in a rural area is somewhat unusual in itself, although Owen (1962) noted that melanic *P. titea* were not first reported from near industrial centers. Melanic *P. titea* should be at a cryptic disadvantage in an area where backgrounds have not been noticeably darkened by pollution. This seems especially true in view of the previously demonstrated preference of these melanics for light backgrounds (Sargent, 1969). However, in spite of what should be a cryptic disadvantage, melanics now comprise a substantial proportion of the *P. titea* population, and must then have some advantage, perhaps a physiological superiority, over typicals. Effects of industrialization, other than observable environmental darkening, may be involved in this situation. Perhaps, for example, the larvae of melanics are better able to tolerate certain chemicals that are being introduced into the environment via air pollution. It may also be that industrialization is reducing selection pressures on cryptic moths by destroying the essential habitat and food supplies of many predators.

Our understanding of the phenomenon of industrial melanism is far from complete. Opportunities for its study are still widely available, especially in North America and I hope these opportunities will not be lost.

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